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The Combing of Cribellar Silk by the Prithine *Misionella mendensis*, with Notes on Other Filistatid Spiders (Araneae: Filistatidae)

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ABSTRACT

We present the first observations of the combing and attaching behavior in the subfamily Prithinae (Filistatidae), taken from *Misionella mendensis*. We compare its web architecture with that of other prithines (*Pritha nana* and *Pikelinia* sp. from Chile) and filistatines (*Kukulcania hibernalis* and *Filistata insidiatrix*). The combing behavior of *M. mendensis* corresponds to the stereotyped type I combing behavior, as is known for other filistatids. However, *M. mendensis* attaches the cribellar segments in a unique way, splitting the cribellar segment longitudinally and pushing each half to the substrate, attaching the silk with the tarsi of both legs IV simultaneously. These stereotyped movements result in web units of a very characteristic structure. We report the same split attachment behavior in the prithine *Pikelinia tambilloi*. We scored these observations into a previous dataset for filistatid relationships. Because of the missing observations on attachment behavior in the North American basal genus *Filistatinella*, the sister group of all other prithines, the evolution of split cribellar strands is a potential synapomorphic characteristic for the Prithinae, or at least the subgroup excluding its basal taxon.

INTRODUCTION

Most web-building spiders produce special, adhesive threads that help retain prey until they are subdued. Cribellar capture threads

consist of a mat of thin fibrils produced by hundreds of minute cribellar spigots, mounted on top of thicker structural lines. For building these cords the spider combs the cribellar fibers using highly stereotyped movements.

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Cribellar silk combing behavior has contributed to phylogenetic hypotheses relating higher groups of spiders (Eberhard, 1988; Lopardo et al., 2004; Griswold et al., 2005). Eberhard (1988) described two different types of combing behavior across many cribellate spider families. In type I, reported for the hypochilid *Hypochilus thorelli* Marx and the filistatid *Kukulcania hibernalis* (Hentz), the combing leg IV rests on the supporting contralateral leg III, but only the leg IV rocks (figs. 1, 7). In type II combing behavior, reported for many cribellate entelegyne spiders (Eberhard, 1988; Griswold et al., 2005) and recently for the Austrochilinae (Lopardo et al., 2004), the combing leg IV rests on the contralateral supporting leg IV, and both legs move together as an almost rigid unit (fig. 2). Additional details of specific behaviors while combing cribellar threads can also be potentially useful in phylogenetic analyses (e.g., Coddington, 1986a; Eberhard, 1988), such as the patterns of alternation of combing legs, legs used in the attachment of threads, and location and disposition of cribellar threads.

The cribellum of spiders of the family Filistatidae is divided (figs. 3, 5), consisting of two plates with several claviform cribellar spigots each (figs. 4, 6; Peters, 1987; Opell, 2002; Griswold et al., 2005). Therefore, this divided cribellum produces double-stranded cribellar threads. Each strand (composed of the fibrils from each cribellar plate) remains distinct when combed, and thus seems to retain its integrity when pulled apart, even by humans (Opell 2002; for details on the morphology of filistatid calamistrum, see Ramírez and Grismado, 1997). Cribellar fibrils built by filistatids lack nodules, and there seems to be some conflicting information related to whether these fibrils are ribbonlike (Eberhard and Pereira, 1993) or just cylindrical (Griswold et al., 2005; also personal obs.).

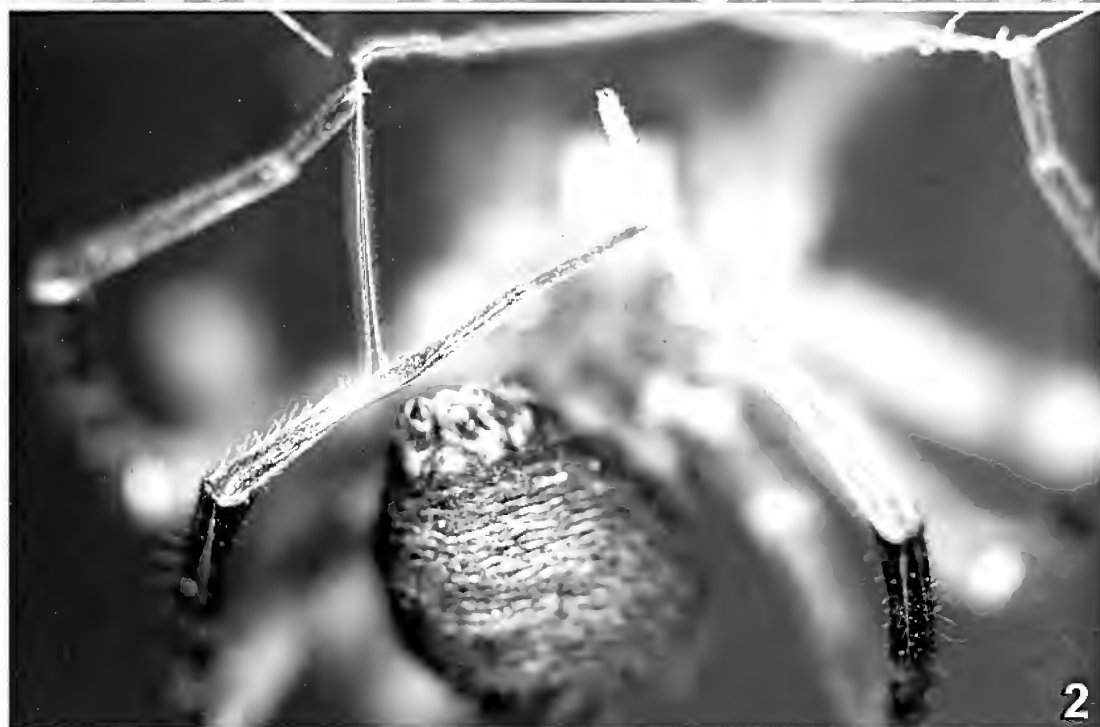
Kukulcania hibernalis (a member of the subfamily Filistatinae) has two different behaviors for attaching the cribellar segments once they are combed (Eberhard, 1988). In one, the abdomen is moved ventrally while the supporting leg III lifts the nonsticky line it was previously holding, and the attachment is directly made by the spinnerets. Neither leg IV manipulates the cribellar segment at the

moment of the attachment, as is the case of all studied cribellate spiders, except *Stegodyphus sarasinorum* Karsch (Eresidae) and *Kukulcania* (see below; Eberhard, 1987, 1988 and references therein; Lopardo et al., 2004). In this type of attachment, a single line made of several adjacent cribellar segments results. In the other type of attachment, the combing leg IV grasps the sticky segment and attaches it to the side of the combing site. Since combing legs tend to alternate, a zigzag pattern of sticky silk results in this second type of attachment. Both behaviors are sometimes used by the same spider, and in general the web patterns are radial, as the spider always combs while moving toward its retreat.

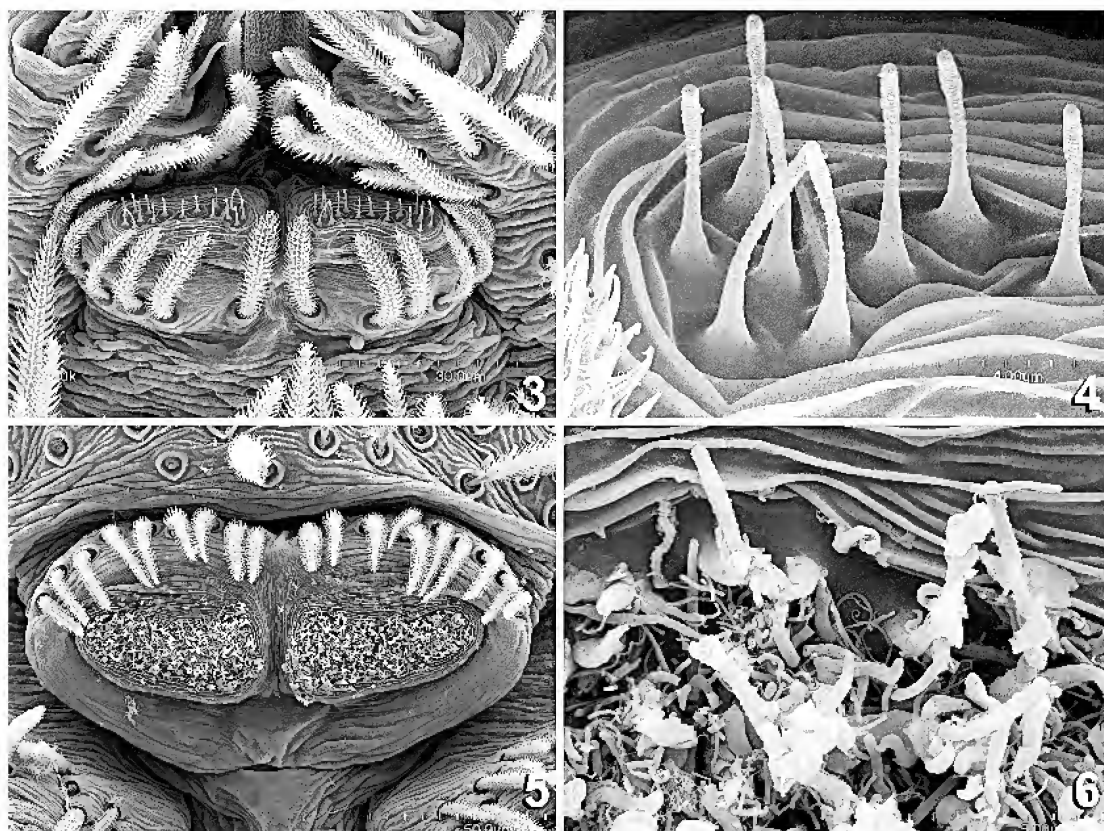
All these patterns and behaviors were observed in one filistatid species and, in the absence of conflicting information, were inferred to describe all Filistatidae. We observed and report here the combing, attachment, and disposition of cribellar silk by *Misionella mendensis* (Mello-Leitão), a member of the filistatid subfamily Prithinae. We also compare the overall web architecture of *Pritha nana* (Simon), *Pikelinia tambilloi* (Mello-Leitão), *Kukulcania hibernalis*, and *Filistata insidiatrix* (Forskål).

MATERIAL AND METHODS

Observations of *Misionella mendensis* were made in Parque Nacional Iguazú, Misiones Province, Argentina, in December 1999 and January 2005. *Kukulcania hibernalis* was observed (but not collected) on houses in Buenos Aires, Argentina. *Pritha nana* was observed in Bolzano, Sud Tirol Region, and *Filistata insidiatrix* in Siena, Toscana Region, Italy, in July 2001. *Pikelinia tambilloi* was collected in Santiago del Estero Province, Argentina (Grismado and Ramírez, 2006), and studied in captivity. Active spiders were observed in the field mostly at night with a flashlight covered with two layers of red cellophane. Captive spiders were placed in Petri dishes and observed under a dissecting microscope. Web samples for SEM were obtained by placing the spider directly on a micro slide or acetate layers placed on Petri dishes. SEM images were taken with a LEO 1430VP microscope at the Department of Biological Sciences (GWU)



Figs. 1–2. The two different types of combing behavior as defined by Eberhard (1988). **1.** Type I combing behavior: the combing leg IV rests on the immobile supporting leg III, and only leg IV moves. *Misionella mendensis* (Filistatidae) from Misiones, Argentina. **2.** Type II combing behavior: the combing leg IV holds on the contralateral supporting leg IV, and both legs move together as an almost rigid unit. *Austrochilus forsteri* Grismado, Lopardo and Platnick (Austrochilidae) from M. N. Contulmo, Chile.



Figs. 3–6. Filistatid cribellum and cribellar spigots. 3–4. *Misionella mendensis*, early spiderling, third dispersing stage, from Misiones, Argentina (SEM preparation MJR-00055). 3. Cribellum. 4. Cribellar spigots. 5–6. *Pritha nana*, female from Bolzano, Italy (SEM preparation MJR-00805). 5. Cribellum. 6. Cribellar spigots.

and a Hitachi S4700 FE microscope at the AMNH SEM facilities. For photography and to facilitate detailed observations we often increased contrast by dusting the webs with cornstarch (Carico, 1977). After observations were complete, we collected the spiders for identification. Vouchers of all observations, photographic slides, and web samples are labeled with acronyms of collector, date, and a sequential number or code, followed by film frame number (e.g., MJR 15.XII.99/3, photo frame 9), and deposited in Museo Argentino de Ciencias Naturales (MACN-Ar, Cristina Scioscia, Buenos Aires).

SPECIMENS: *Pritha nana*: ITALY: Reg. Sud Tirol: Bolzano: Bolzano, 7–10.VII.2001, M. Ramírez, 5♀, 22 immatures, 2 eggsacs (MACN-Ar 10376; SEM preparations MJR-00804–00805); 1♀, same data (MACN-Ar

10377); 1♀, same locality, MJR 9.IV.01/2 (MACN-Ar; SEM preparation MJR-00270; escaped in the lab).

Filistata insidiatrix: ITALY: Reg. Toscana: Siena: 4 km S San Gimignano, Fattoria Voltrona, 12.VII.2001, M. Ramírez, 7♀, 6 immatures, 5–6 eggsacs (MACN-Ar 10378; SEM preparations MJR-00798–00803, 00835); 1♀, same data (MACN-Ar 10379).

Pikelinia tambilloi: ARGENTINA: Santiago del Estero: P. Nac. Copo, settlers area, 22–24.II.2004, C. Grismado, A. Ojanguren, F. Labarque, L. Compagnucci, 1♀ (MACN-Ar 10723, preparation MJR-00971; reared in lab until 14.VI.2005); 1♀ (preparation MJR-01030, voucher escaped).

Misionella mendensis: ARGENTINA: Misiones: P. Nac. Iguazú, área Cataratas, 11–16.XII.1999, M. Ramírez and L. Lopardo, 1♀,



Figs. 7–8. Combing and attaching behavior for *Misionella mendensis* (Misiones, Argentina). 7. Combing behavior, note the right combing leg IV resting on the left supporting leg III. 8. *M. mendensis* in a posterior view attaching the split cribellar thread using both legs IV.

1 eggsac (MACN-Ar 10354, MJR 11.XII.99/3); 1♂ (MACN-Ar 10355, photos MJR 11.XII.99/2, photo frames 0–4); 1♀ (MACN-Ar 10356, MJR 11.XII.99/30, photo frames 8–10); 1♀ with spiderlings (MACN-Ar 10366, SEM preparations MJR-00053–00055); 1♀ with spiderlings (MACN-Ar 10370, SEM preparation MJR-00056); 1♀ (MACN-Ar 9851); 1♀ with eggs (MACN-Ar 9852); 1♀ with exuviae of spiderlings, 1♀ with spiderlings (MACN-Ar 9853); 1♀ with recently hatched spiderlings (MACN-Ar 9854; SEM preparation MJR-00060, 00062–00063); 2♂, 1♀ (MACN-Ar 10357); 5♂ (MACN-Ar 10358); 5♂, 4♀ (MACN-Ar 10359); 1♀ (laid eggsac in lab, then died while molting, MACN-Ar 10360); 1♀ (MACN-Ar 10361); 3♀; (MACN-Ar 10362); 1♀ exuvia, 1 eggsac with exuviae of spiderlings (MACN-Ar 10363); 2♀ (MACN-Ar 10364); 1♀ (died while molting, MACN-Ar 10365); 1♀ with spiderlings and eggs (MACN-Ar 10367); 1♀ with spiderlings (MACN-Ar 10368); 1♀ with spiderlings (MACN-Ar 10369); 1♀ with spiderlings (MACN-Ar 10372); 1♀ with eggs (MACN-Ar 10373); 3 immatures (MACN-Ar 10375); 1♀ with eggs (MACN-Ar 10371); 1♀ with hatched eggsac (MACN-Ar 10374); 17–22.I.2005, C. Grismado, L. Lopardo, L. Piacentini, A. Quaglini and G. Rubio, 1♂ subadult; 3♀; 1♀ (SEM preparation LL-G).

RESULTS

COMBING BEHAVIOR

Misionella mendensis has nocturnal habits, and is very common in houses in Misiones Province in Argentina (Ramírez and Grismado, 1997). Webs are scattered over brick walls, and in each web new threads are laid over older ones, producing a dense mesh of silk. Webs of different individuals usually overlap. When the spider combs, the tip of the combing leg IV rests on the tibia or sometimes the metatarsus of the supporting leg III, and only the leg IV rocks (figs. 1, 7). Eberhard (1988) describes the same leg arrangement for *Kukulcania hibernalis*, terming it type I combing behavior. The combing leg IV rocks so fast that it becomes blurry to the eye. The spider is stationary while combing, it moves only after attaching the sticky silk segment. We report the same combing behavior for *Pikelinia tambilloi*.

ATTACHMENT AND DISPOSITION OF CRIBELLAR SILK

The double-stranded cribellar threads combed by filistatids are handled together as entire, undivided segments by *Filistata insidiatrix* (Peters 1987), and *Kukulcania*, since each time the attaching behavior is performed, the

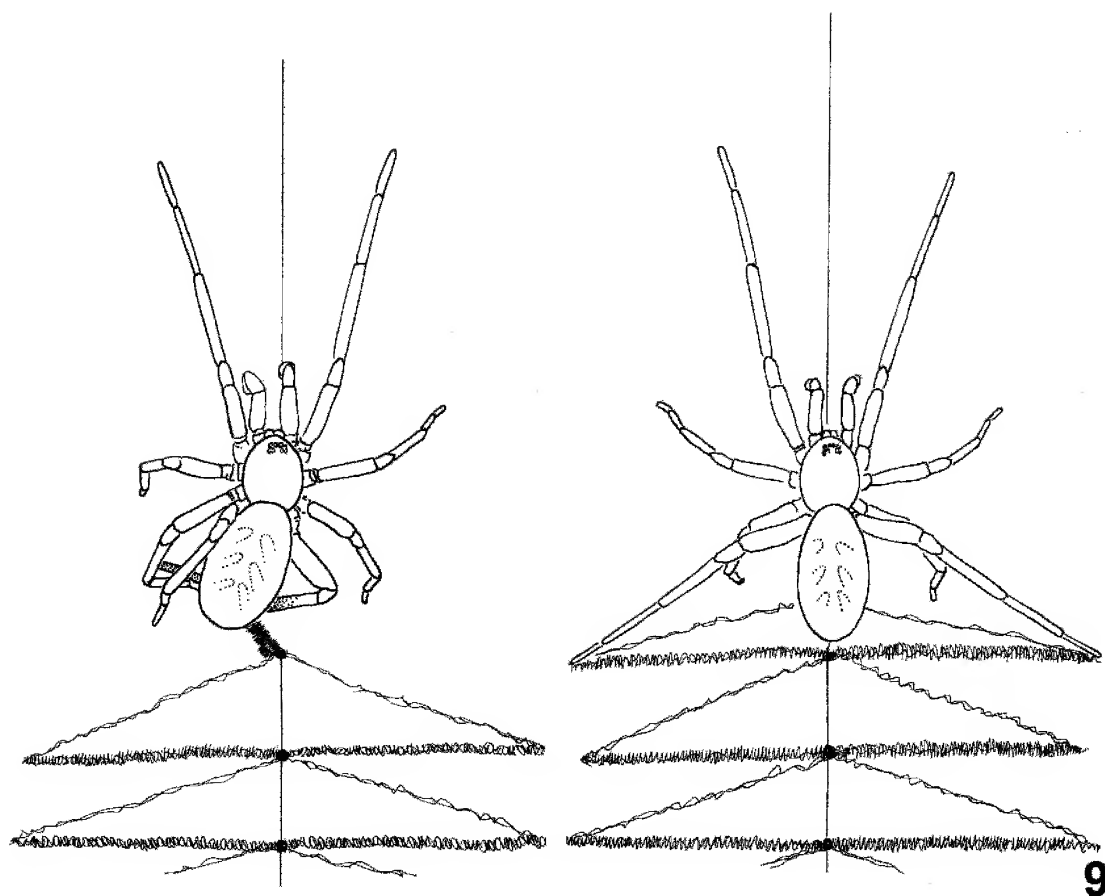


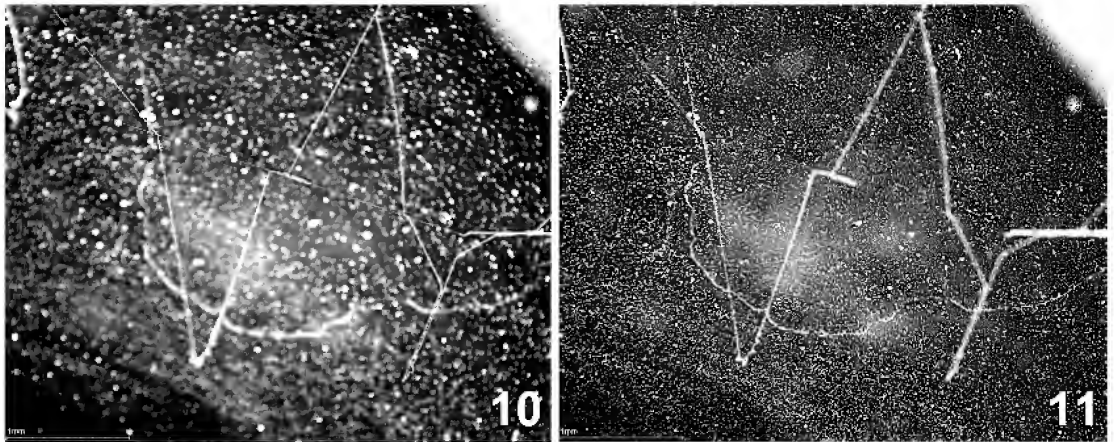
Fig. 9. Schematic drawing showing the attaching behavior of the prithine *Misionella mendensis* once the cribellar segment is combed, splitting both halves of the cribellar thread, and the disposition of the sticky silk and the foundation line. (Left, drawn from photography [from fig. 7]; right, composed from fig. 8.)

double stranded segment is attached at the same position on the foundation line, and the left and right cribellar strands run parallel to each other.

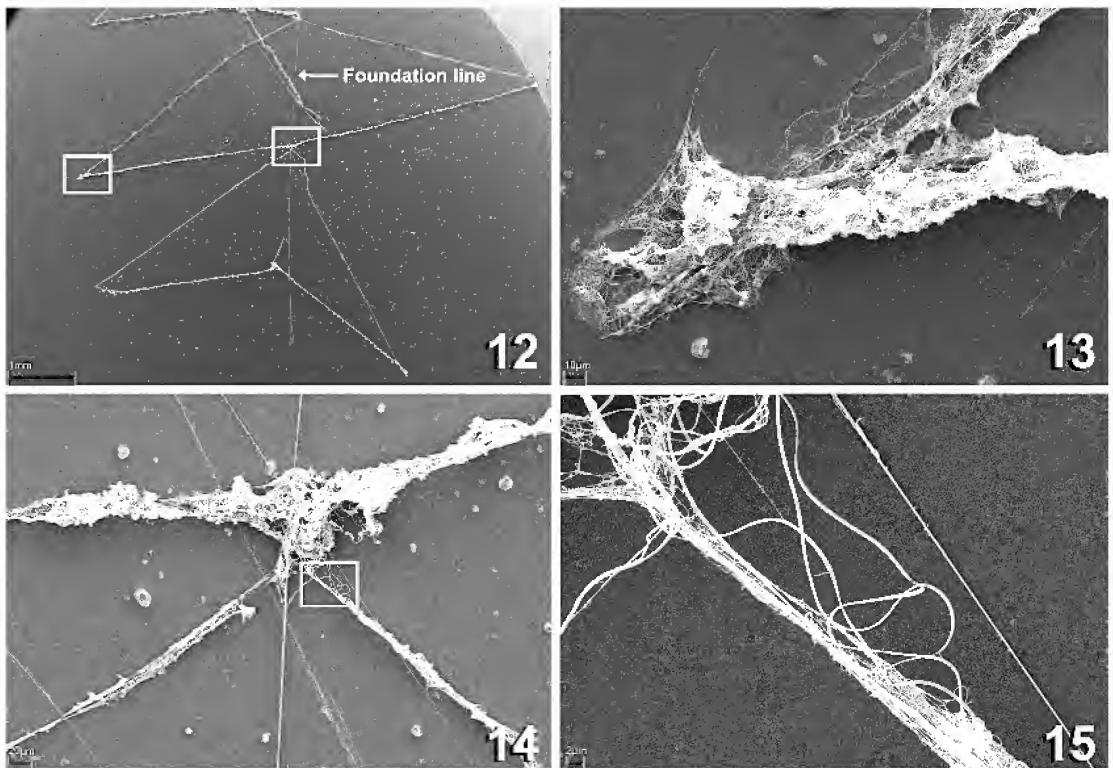
But a different behavior is observed in *Misionella* and *Pikelinia*. As in *Kukulcania*, the spiders also move toward its retreat while spinning, using a foundation line elevated from the substratum as a guide (figs. 10, 11). Once a sticky segment is combed, the cribellar silk production ceases, and the spider grasps the double-stranded cribellar segment with both legs IV. It then splits the segment to exactly opposite sides, attaching each end to the substrate with the tip of the tarsi, thus producing a transverse line made of two single-stranded cribellar threads (figs. 8, 9).

The lateral attachments made with the legs are stuck to the substrate by contact adhesion only (fig. 13). As the legs IV spread, the support lines continue to be drawn out of the spinnerets. After attaching the cribellar segment, the spider moves forward (angling the supporting lines anteriorly) and attaches again on the foundation line, forming an isosceles triangle (figs. 12, 14–16). Combing of a new cribellar segment then resumes. Webs of *Misionella mendensis* are thus a dense mesh made of old and new radial lines oriented toward a retreat, and filled with transverse cribellar threads (figs. 17, 18).

The web of the prithine *Pritha nana* (fig. 19) is similar to that of *Misionella mendensis* and *Pikelinia*, with a retreat surrounded by a dense



Figs. 10–11. Cribellar silk in *Pikelinia tambilloi* from Santiago del Estero, Argentina, on a Petri dish. **10.** Detail of foundation line elevated from the substratum and used as a guide. Note the foundation line, the cribellar thread, and the point of split in it. **11.** Same, detail on the attachment point of the cribellar thread below the plane of the foundation line.



Figs. 12–15. Structure of a cribellar thread in *Misionella mendensis* (SEM preparation LL-G). **12.** Detail of two structural units of sticky segments from a web sample. Note the foundation line, the cribellar thread, and the point of split in it. **13.** Same, detail on the attachment point of the cribellar thread with legs IV. **14.** Same, detail of the point of split in the cribellar double-stranded thread. **15.** Detail of the split supporting lines.



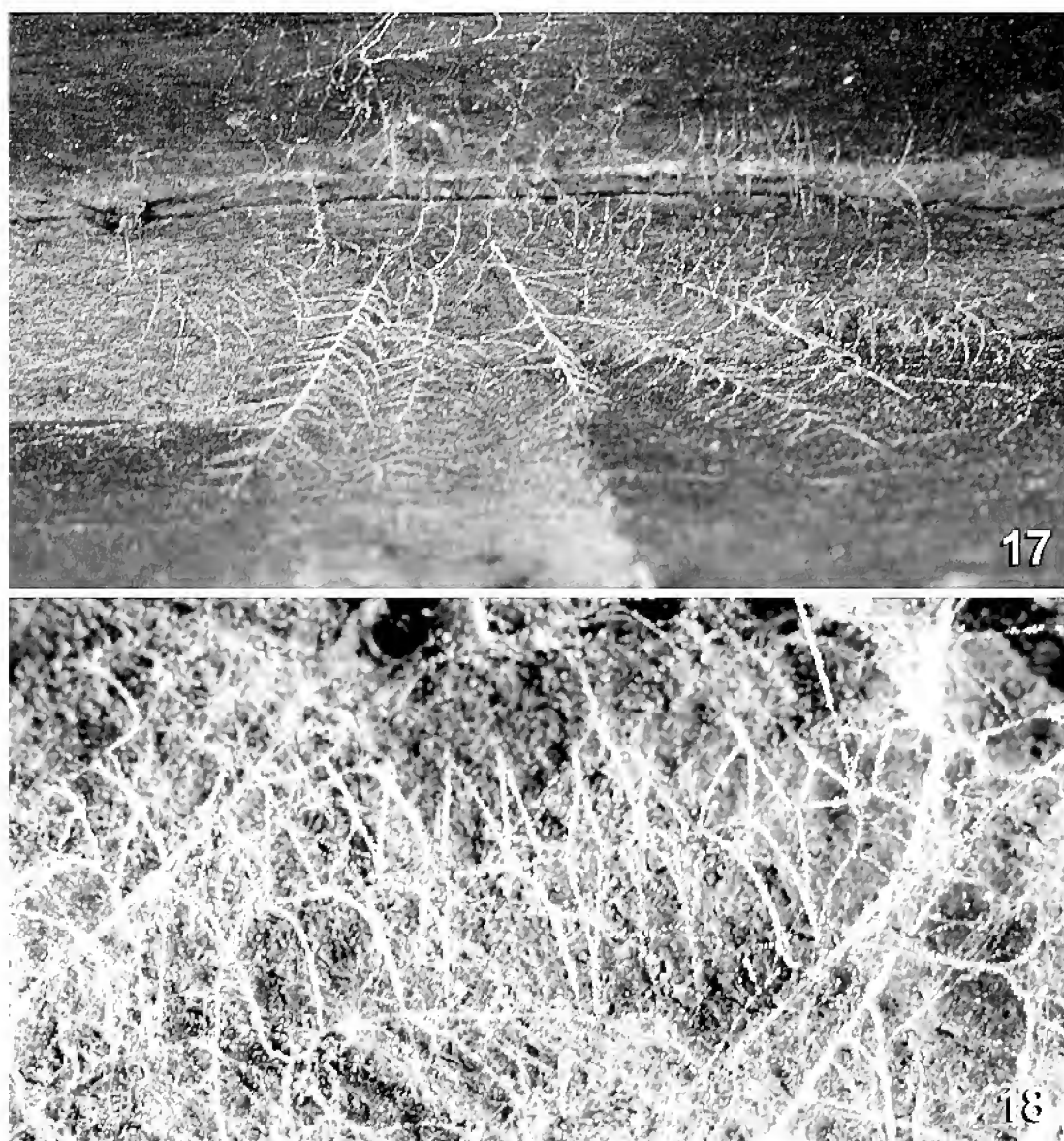
Fig. 16. Cribellar silk in *Pikelinia tambilloi* from Santiago del Estero, Argentina, on a Petri dish. Note the structural units of split cribellar threads.

mesh of radial foundation lines filled with transverse, single-stranded cribellar silk (MJR, personal obs.). Because the structural units are the same, we expect *P. nana* to comb and attach the cribellar threads as do *Misionella* and *Pikelinia*, using a type I combing behavior, and splitting the cribellar threads using both legs IV.

WEB STRUCTURE IN *FILISTATA* AND *KUKULCANIA*

The webs of the filistatines *Kukulcania hibernalis* (fig. 20) and *Filistata insidiatrix* have a more definite funnel-like retreat. Eberhard (1988; also personal obs.) described the type I combing behavior of *Kukulcania hibernalis*, and we report here the same for *Filistata insidiatrix*. Older webs typically have a dense mesh of superimposed lines without an apparent pattern except at the margins, where

the functional capture units are placed (figs. 21, 22, 25, 26). Webs made by young spiders are smaller and cleaner, and the radial arrangement of sticky lines is more evident (figs. 23, 24, 27, 28). A radial foundation line leads from the retreat to the periphery, is typically slightly elevated from the substrate, and supports the cribellar segments added toward the retreat in a looped fashion (at least in *Kukulcania*; Opell, 2002). Eberhard (1988) reported that from time to time *Kukulcania hibernalis* laid cribellar strands directly to the substratum using one leg IV, producing a zigzag pattern of cribellar threads at the sides of the foundation line. We did not observe this zigzag cribellar pattern on either older (figs. 25, 26) or younger webs (figs. 27, 28) suggesting that the relative frequency of this attachment behavior might be somehow plastic within the same species.



Figs. 17–18. *Misionella mendensis* (Misiones, Argentina) web's general appearance. **17.** Note the radial disposition of the foundation lines toward the retreat, and the transversal cribellar threads. **18.** Detail of web. Note the old lines under the new ones.

CLADISTIC ANALYSES

We scored the data matrix of filistatid spiders by Ramírez and Grismado (1997) for a binary character expressing the two types of attachment of the double-stranded sticky lines (0: entire; 1: split). *Filistata* and *Kukulcania* and the outgroup taxa were assigned state 0; *Pikelinia*, *Misionella*, and *Pritha* state 1; the

state of all other filistatid genera (*Sahastata*, *Afrofilistata*, *Andoharano*, *Filistatinella*, *Filistatoides*, *Lihuelistata*, *Yardiella*, *Wandella*) is unknown (missing entries). The analyses of the data matrix with equal and implied weights (using the same analytical procedures as in Ramírez and Grismado, 1997) yields the same cladograms unaltered (fig. 29) (length = 48 steps; Fit = 213.5 [under concavity K = 3];



Figs. 19–20. Filistatid spiders. **19.** *Pritha nana*, female from Bolzano, Italy. **20.** *Kukulcania hibernalis*, male from Buenos Aires, Argentina.

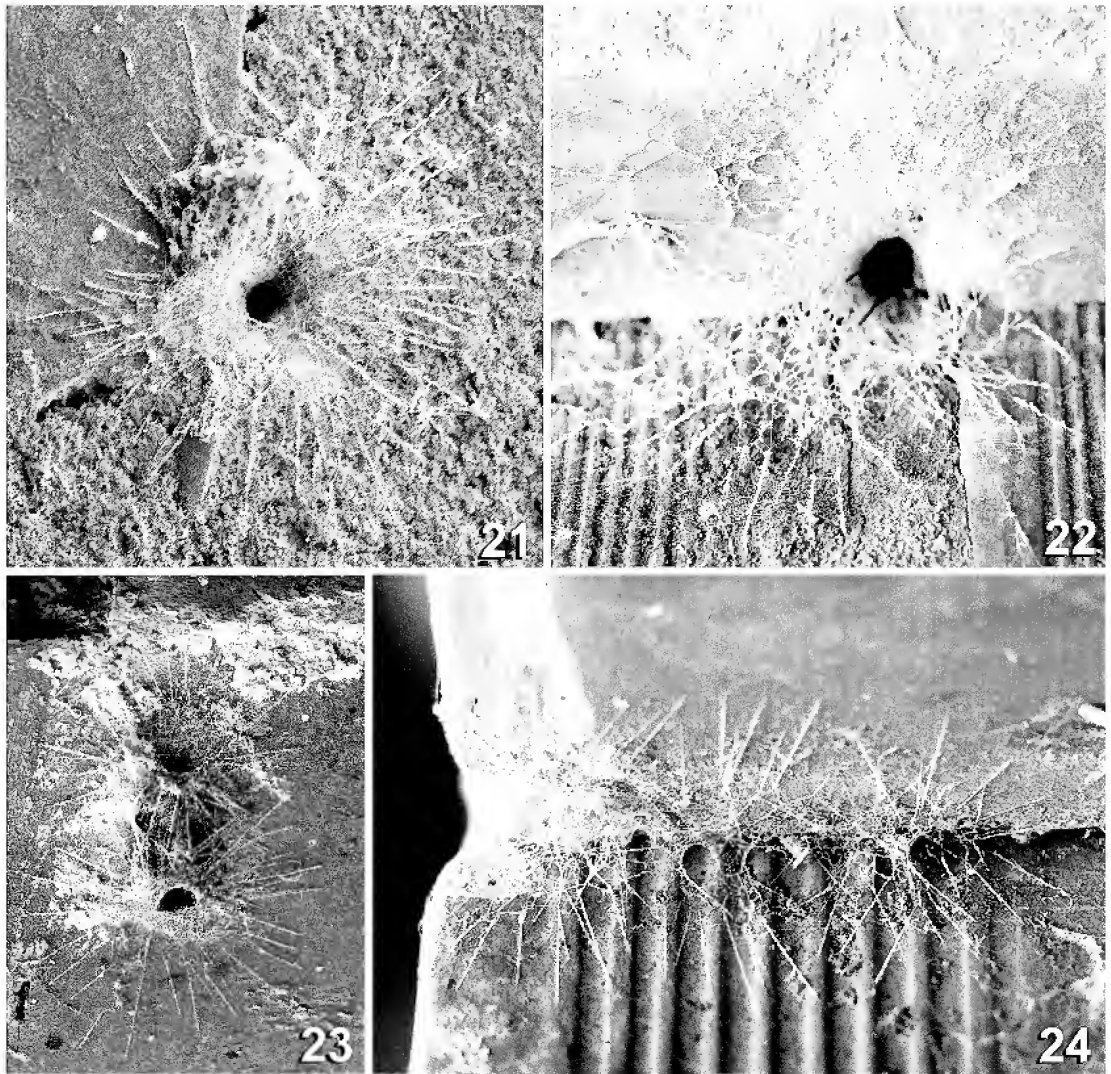
Rescaled Fit = 84%; CI [informative characters only] = 0.78; RI = 0.86). The evolution of the two types of attachment of the double stranded sticky lines was optimized on the cladogram on figure 29.

DISCUSSION

Both filistatines and prithines comb in the same stereotyped manner—with the tip of the combing leg IV resting on the tibia of the supporting leg III—using the type I combing behavior of Eberhard (1988). They also move toward the retreat as they produce cribellar lines, and their funnel webs exhibit a similar general pattern of radially placed capture threads leading to a central retreat, although filistatines place the cribellar threads mainly running along the foundation line. The highly modified split capture-threads of *Misionella*, *Pikelinia* and *Pritha* seem to be further transformations of this basic pattern. Although we have not observed the construction of capture units in *Pritha*, their structure indicates that they use a behavior similar to that of *Misionella*. As we expected, the cladistic analysis shows that this thread structure and attaching behavior is a potential synapomorphy for the Prithinae, or at least the subgroup excluding its basal taxon (fig. 29). The combing and attachment behavior of the North American basal genus *Filistatinella*, the sister group of all other prithines, is unknown, and is essential for the understanding of the evolution of split cribellar strands within Filistatidae.

Although members of some other cribellate families possess divided cribella as well, none of them are known to split and attach cribellar silk using both legs IV in this unique behavior described for prithine spiders. Across cribellate spiders, legs IV show different degrees of participation in attaching cribellar threads. In some they are not involved at all in making attachments, not even grasping any line (sticky or nonsticky); instead, thread attachments are made directly by the spinnerets—e.g., Austrochilinae (Lopardo et al., 2004), Mallos (Dictynidae, Eberhard, 1982), *Hypochilus*, *Kukulcania* (occasionally), *Psechrus*, and *Tengella* (Eberhard, 1987, 1988). Sometimes both legs IV grasp a nonsticky line (usually the radius of an orb web) on either side of the attachment point (e.g., Uloboridae [Eberhard, 1972, 1988] and Deinopidae [Coddington, 1986a]) or one leg IV occasionally grasps the nonsticky line held by ipsilateral leg III (e.g., *Tengella* [Eberhard, 1988]). Finally, they can directly manipulate cribellar threads, either with one leg IV (e.g., *Stegodyphus* and *Kukulcania* [occasionally, Eberhard, 1987, 1988]) or both legs IV (e.g., *Misionella*, and probably *Stegodyphus* [Eberhard, 1988]), and the attachment is made by using these legs to press the cribellar silk against the substrate, without intervention of the spinnerets.

The factors determining which combing leg will comb next are unknown for filistatids. There are no clear data on how often filistatids alternate their combing legs. In austrochilines, the leg III used in the attachment consistently determines that the ipsilateral leg IV will comb the next segment (Lopardo et al., 2004), and in

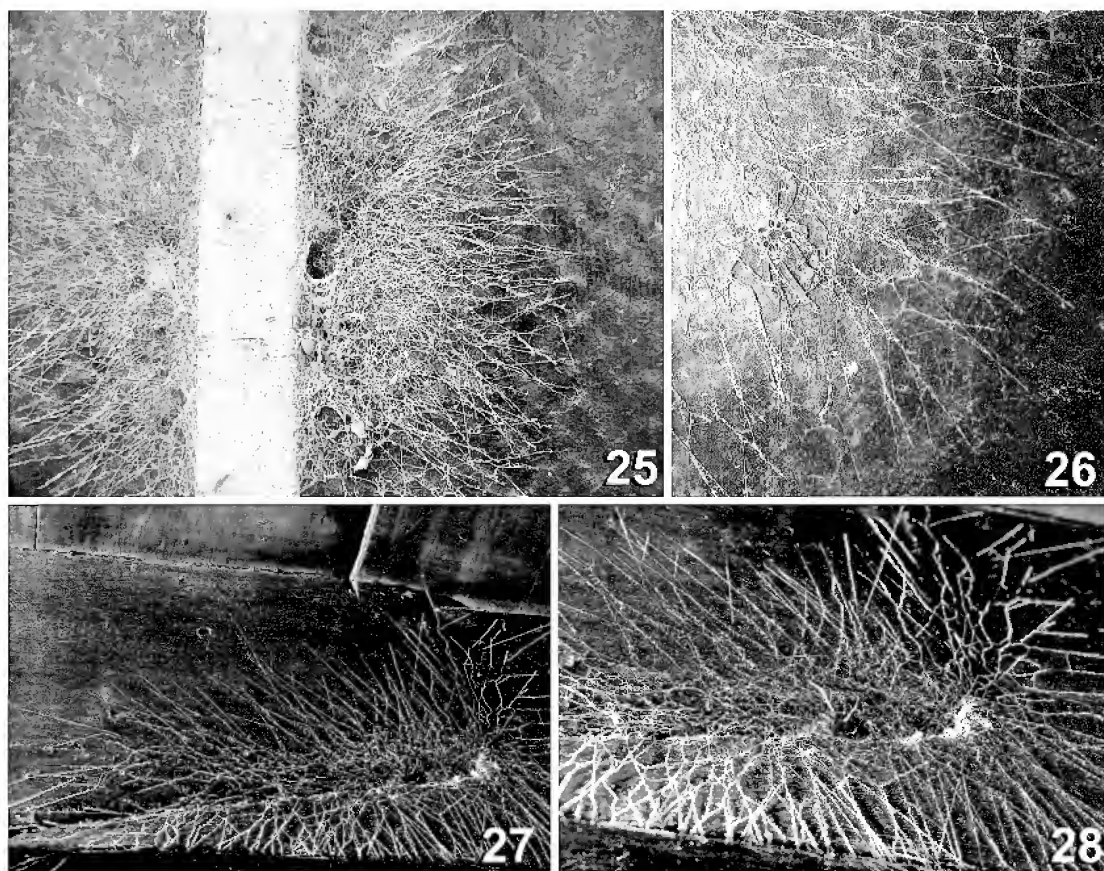


Figs. 21–24. *Filistata insidiatrix* (Siena, Italy), webs on a brick wall. **21–22:** Webs of adults. Note the mesh of overlapped threads. **23–24:** Webs of juveniles. Note the radial lines with cribellar thread on their edges.

Uloboridae and Deinopidae, the outer leg IV will start combing the next segment, and then it will switch (or not) to the inner leg within the same segment of cribellar silk (Eberhard, 1972, 1988; Coddington, 1986a), but these factors that affect the combing legs in these spiders would not be applicable for prithines. No leg III participates in the attachments, and there is no “outer” or “inner” leg when combing toward the retreat in prithines. Thus, we still do not know what action precedes the alternation of combing legs in

this subfamily, although in filistatines the leg III involved in at least one type of attachment might probably indicate the next combing leg.

While details in the evolution of web architecture in higher groups of spiders remain obscure due to lack of features among webs that can be classed as homologous, behaviors associated with their construction and the production of sticky silk might help to elucidate this problem (e.g., Coddington, 1986a,b; Eberhard, 1982, 1990; Griswold et al., 1998, 1999, 2005; Hormiga et al., 1995;



Figs. 25–28. *Kukulcania hibernalis* (Buenos Aires, Argentina), webs on houses. **25.** Web of adult, general appearance. **26.** Same, detail on the edge of the web. **27–28.** Webs of juveniles on a wooden wall. Note the radial lines with cribellar thread on their edges.

Scharff and Coddington, 1997). In doing so, these similar behaviors can reveal homologous structures embedded in extremely different web architectures. Conversely, progress in the knowledge on how webs are built can help us to deduce from the finished web which behaviors were used to create it.

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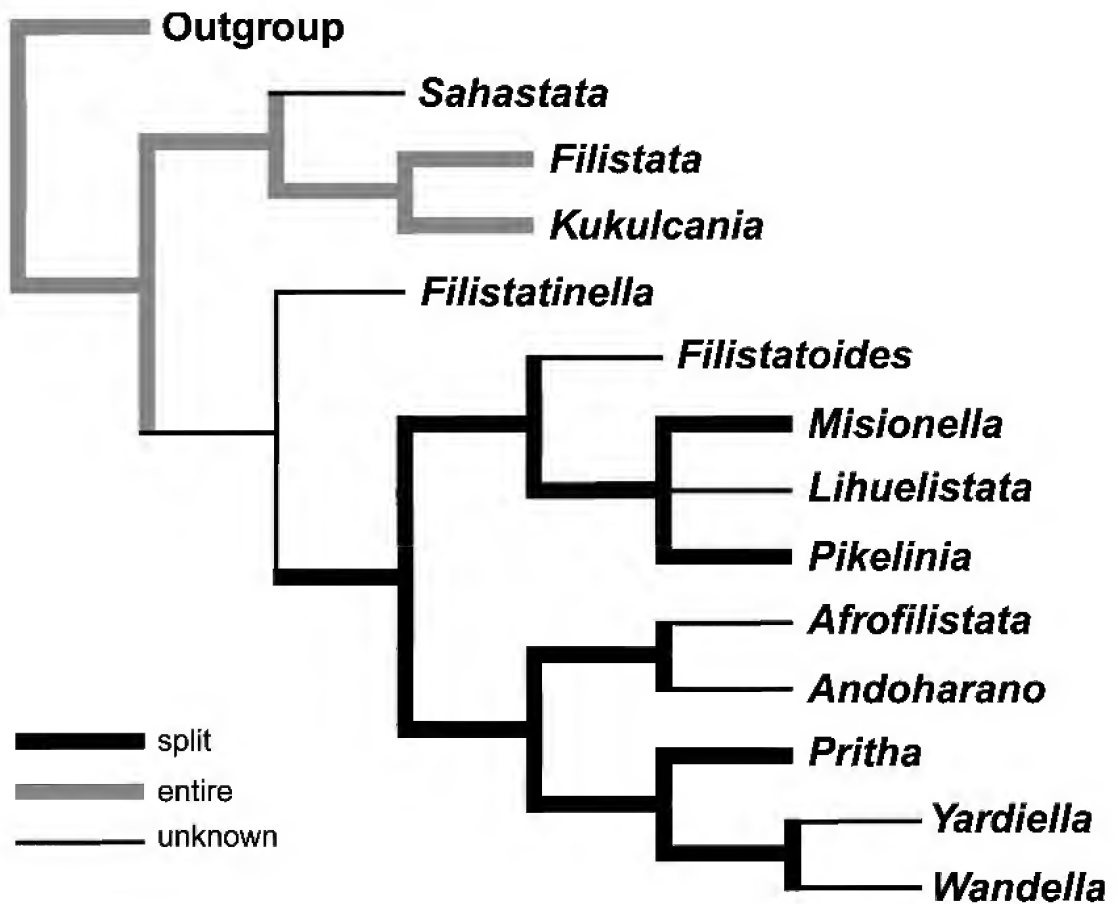


Fig. 29. Evolution of the different types of attachment of double-stranded sticky lines optimized on the cladogram of generic relationships within Filistatidae, according to Ramírez and Grismado (1997) and our analysis. Note the ambiguous optimization on the Prithinae node.

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